man intervention on bald eagle habitat. J. Wildl. Manage. 55:290–293.

SKAGEN, S. K. 1980. Behavioral responses of wintering bald eagles to human activity on the Skagit River, Washington. Pages 231–241 *in* R. L. Knight, G. T. Allen, M. V. Stalmaster, C. W. Servheen, eds. Proc. Wash. Bald Eagle Symp. The Nature Conservancy, Seattle.

———, R. L. KNIGHT, AND G. H. ORIANS. 1991. Human disturbance of an avian scavenging guild. Ecol. Appl. 1:215–225.

SMITH, T. J. 1988. The effect of human activities on the distribution and abundance of the Jordan Lake-Falls Lake bald eagles. M.S. Thesis, Virginia Polytech. and State Univ., Blacksburg. 100pp.

STALMASTER, M. V. 1983. An energetics simulation model for managing wintering bald eagles. J. Wildl. Manage. 47:349–359.

———. 1987. The bald eagle. Universe Books, New York, N.Y. 227pp.

———, AND J. L. KAISER. 1997. Winter ecology of bald eagles in the Nisqually River drainage, Washington. Northwest Sci. 71:214–224.

———, AND J. R. NEWMAN. 1978. Behavioral responses of wintering bald eagles to human activity. J. Wildl. Manage. 42:506–513.

U.S. FISH AND WILDLIFE SERVICE. 1986. Recovery plan for the Pacific bald eagle. U.S. Fish and Wildl. Serv., Portland, Oreg. 160pp.

WATSON, J. W. 1993. Responses of nesting bald eagles to helicopter surveys. Wildl. Soc. Bull. 21: 171–178.

Received 26 September 1996.
Accepted 19 July 1997.
Associate Editor: Murphy.

REPRODUCTIVE SUCCESS OF BALD EAGLES IN INTERIOR ALASKA

ROBERT J. STEIDL,[1] Department of Fisheries and Wildlife, Oregon Cooperative Wildlife Research Unit, Oregon State University, 104 Nash Hall, Corvallis, OR 97331-3803, USA
KARIN D. KOZIE, Wrangell-St. Elias National Park, P.O. Box 439, Copper Center, AK 99588, USA
ROBERT G. ANTHONY, U.S. Geological Survey, Oregon Cooperative Wildlife Research Unit, Oregon State University, 104 Nash Hall, Corvallis, OR 97331-3803, USA

Abstract: We compared productivity and nesting success of 2 adjacent populations of bald eagles (*Haliaeetus leucocephalus*) near the northern limits of their range in interior Alaska during 1989–94. Productivity ($\bar{x} \pm$ SE young fledged/occupied territory) and nesting success differed between populations; pairs in the Gulkana River basin had higher productivity (0.86 ± 0.05, $n = 274$) and nesting success (59%) than those in the Copper River basin (0.71 ± 0.04, 48%, $n = 471$; $P < 0.02$). Productivity varied both annually and spatially within each basin ($P < 0.001$). However, brood sizes of successful nests were identical for both basins (1.48 ± 0.03), suggesting that variability in productivity resulted largely from differences in nesting success. Patterns of variability in reproductive success within a territory also were similar for both populations. Pairs that were successful one year fledged more offspring, were more likely to be successful, were more likely to reoccupy the same territory, and were less likely to change nest locations the following year compared to pairs that were unsuccessful the previous year ($P < 0.025$ for all comparisons). Most nesting failure (92%) occurred during incubation when weather conditions tend to be most severe. However, reproductive success was not negatively correlated with severity of spring weather (temp or rainfall) or strongly correlated with prey abundance during brood rearing. We hypothesize that annual and spatial variability in reproductive success of these northern bald eagle populations may be associated with variation in prey availability, especially before and during incubation.

J. WILDL. MANAGE. 61(4):1313–1321

Key words: Alaska, bald eagle, breeding success, Copper River, demography, Gulkana River, *Haliaeetus leucocephalus*, nesting, nesting success, prey abundance, productivity, reproductive success.

Reproductive success of populations may vary because populations are affected differentially by resource availability, human disturbance, weather, or other facets affecting habitat quality. Understanding processes that explain differences in reproduction can provide insights into how these factors influence populations and also can provide direction to biologists con-

---

[1] Present address: School of Renewable Natural Resources, 325 Biological Sciences East, University of Arizona, Tucson, AZ 85721, USA.

cerned with recovery or management of sensitive or endangered species. When resources for protection of threatened or endangered species are limited, one approach is to concentrate conservation measures in areas where fitness and the likelihood of population persistence are highest.

Bald eagles nest predominantly near estuaries, lakes, rivers, and coastlines throughout much of North America (Stalmaster 1987:119), but reproductive success varies temporally and spatially throughout their range (Sprunt et al. 1973, Grubb et al. 1983, Gerrard et al. 1992). Differences in reproductive success of bald eagle populations may reflect differences in habitat quality, which includes factors such as availability of prey and nesting habitat, or differences in environmental or anthropogenic pressures to which these populations are exposed.

Bald eagles reach their highest abundances along coastal Alaska (ca. >30,000 individuals, Schempf 1989). However, several smaller populations nest in interior Alaska near the northern limits of the species' range (ca. 525–725 breeding pairs, Ritchie and Ambrose 1996). We assessed reproductive success of 2 adjacent populations of bald eagles in the Copper River drainage of interior Alaska. We examined how reproductive success of populations near their biogeographical limit varied with geographic location, year, spring weather conditions, prey availability during brood rearing, and reproductive history of individual nesting territories.

Our study was funded by the Bureau of Land Management, National Park Service, and U.S. Fish and Wildlife Service, Alaska. J. Lee, A. Lee, and J. Hannah piloted survey planes, and F. Bird, J. Bernatowicz, and T. Bowman assisted with surveys. S. Ambrose provided baseline data on the location of eagle nests and P. Schempf provided productivity data for the Lower Copper River region in 1989 and 1990. N. Szarzi, Alaska Department of Fish and Game, provided estimates of salmon escapement. We thank W. D. Edge, S. L. Olson-Edge, and K. J. Jenkins for comments on our paper.

STUDY AREA

The Gulkana National Wild River is a free-flowing wilderness river in southcentral Alaska that originates north of Summit Lake and south of the Alaska Range (63°07'N, 150°30'W) and flows south into the larger Copper River. We divided the Gulkana Basin into 3 subbasins based on its 3 major tributaries: Main Stem, Middle Fork, and West Fork. The Main Stem of the Gulkana River is characterized by clear waters with a combination of whitewater rapids, riffles, and meandering reaches. The Gulkana's 2 other major tributaries, the Middle and West forks, are similar to the Main Stem, but meander considerably more. Higher elevation areas of all subbasins (>1,000 m) were treeless and vegetated with a moist tundra community. Lower elevation areas were dominated by boreal forest, composed principally of black (*Picea mariana*) and white spruce (*P. glauca*), with some balsam poplar (*Populus balsamifera*), quaking aspen (*P. tremuloides*), and paper birch (*Betula paperifera*). Eagles nested atop all these species except black spruce, which do not grow large enough to support nests. Nests were built at elevations between 400 and 960 m and were usually located near water, the only area where trees grow large enough to support nests. Hundreds of lakes dot these subbasins and are especially numerous in the West Fork subbasin. The Gulkana and its tributaries support anadromous runs of chinook (*Oncorhynchus tshawytscha*) and sockeye salmon (*O. nerka*), as well as resident populations of arctic grayling (*Thymallus arcticus*) and rainbow trout (*O. mykiss*).

The Copper River is also free-flowing but differs from the Gulkana in that it is fed predominantly by glacial runoff. Hence, flowing waters in the Copper Basin are extremely turbid. Our study area in the Copper Basin extended from Copper and Tanada lakes (62°25'N, 143°25'W) south along the Copper River to Miles Lake, east along the Bremner River to its confluence with the Little Bremner River, and west along the Tasnuna River to the Woodworth Glacier. Based on physiographic differences, we divided the basin into 3 subbasins: the Upper, Middle, and Lower Copper rivers. The Upper Copper River extends from Copper and Tanada lakes to the confluence of the Copper and Chistochina rivers; the river here is relatively narrow and the river corridor is dominated by white and black spruce. The Middle Copper River extends from the Chistochina River south to the confluence of the Chitina River, and includes areas of the Lower Tonsina River; here the river becomes wider and more braided, and surrounding areas contain both spruce and balsam poplar. The Lower Copper River extends from the Chitina River south to Miles Lake and includes the Tasnuna and Bremner rivers; here the river continues to widen and braid with steep canyons on either side. Vegetation in the Lower Copper River subbasin begins to exhibit coastal influences. Black cottonwood (*Populus trichocarpa*) dominated the river corridor and white spruce occurred more commonly in nearby upland areas. The Copper River and many of its tributaries support anadromous runs of chinook and sockeye salmon. These basins support 2 of the northernmost breeding populations of bald eagles (Ritchie and Ambrose 1996).

The breeding season in this region is short compared to lower latitudes (Bent 1937, Gerrard and Bortolotti 1988:76); therefore, eagles face a considerable time constraint in which to complete nesting. In general, eagles arrive in early April, begin nesting in late April and early May before winter ice-breakup, young begin to fledge by mid-August, and both adults and young begin to leave their nesting territories in early September. Nesting is consistently later in the Lower Copper River subbasin compared to other subbasins, probably because of numerous nearby glaciers that delay snow melt and maintain a winter-like condition several weeks longer than more northern areas. One biologically important environmental characteristic of this region is the extended daylight period from May through August, which approaches 24 hours. Human activity is negligible throughout most of the Copper River and Gulkana River basins. However, use by whitewater rafters and anglers becomes appreciable along the Main Stem Gulkana River after eggs hatch in early June: during 1989–93 an average of 919 groups per year floated this reach between 1 June and 11 September (Steidl 1995).

METHODS

Aerial Surveys

We flew 2–3 aerial surveys each year between 1989 and 1993 in the Gulkana Basin and 1989–94 in the Copper Basin. In 1989, we began with 30–50 previously known territories in each basin and increased our sample as we found new territories in subsequent years. We flew occupancy surveys in early to mid-May to determine which territories were occupied: those with an incubating adult, an attending pair of adults, a clutch of eggs (Postupalsky 1974). During 1989 and 1990 we surveyed a sample of occupied nests in the Gulkana Basin (n = 59 for both years combined) soon after peak hatching to estimate the proportion of failures that occurred during incubation. We flew productivity surveys in late-July to mid-August to determine the number of occupied territories with young. A pilot and single observer flew surveys using a Piper Super Cub. We examined the accuracy of our aerial brood counts with ground checks at 86 nesting attempts; counts agreed 100%.

Statistical Analyses

During surveys, we found 53 nests (16 on the Gulkana, 37 on the Copper) that contained young during productivity surveys that had not been found earlier during occupancy surveys. We included these data only when examining brood sizes of successful nests; all other analyses were based on territories that had been observed during both surveys.

We examined reproductive success using productivity (young fledged/occupied territory), brood size (young fledged/successful territory), and nest success (% pairs fledging ≥1 young) for each year a territory was occupied, and also examined rates of territory occupancy. Because reproductive parameters were collected from the same nesting territories each year, data from the same territory may not have been independent among years. Therefore, to evaluate the associations between river basin, subbasin, and year with productivity and brood size as response variables, we used a split-plot analysis of variance (ANOVA) with basin and subbasin as whole-plot factors, year as a subplot factor, and considered territory as a random effect. To evaluate the associations between river basin, subbasin, and year with nest success and territory occupancy as response variables, we used logistic regression, and scaled variance estimates by model deviance when necessary to account for overdispersion (Collett 1991). To calculate rates of territory occupancy (occupied/surveyed), we considered territories the year they were initially occupied and thereafter. We used contingency tables to compare reproductive and nesting activity within territories between consecutive years. Lastly, we used Pearson correlations to examine associations between productivity and nest success with (1) average ambient temperature and total precipitation in May for all years available for each subbasin, and (2) total escapement of chinook and sockeye salmon estimated aerially by basin (N. Szarzi, Alaska Dep. Fish and Game, unpubl. data).

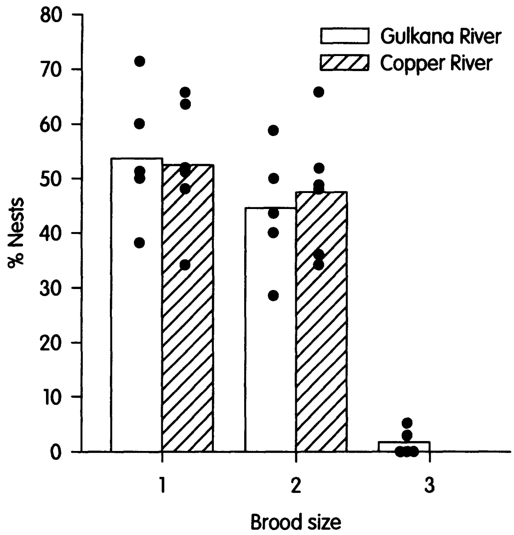

Fig. 1. Distribution of brood sizes of bald eagles from the Gulkana (n = 177; 1989–93) and Copper rivers (n = 263; 1989–94), Alaska. Each point represents brood size for a given year; bars represent brood size for all years combined.

Table 2. Split-plot ANOVA model describing the effects of river basin, subbasin, and year on the number of young fledged per occupied nest (n = 745) for bald eagles in the Gulkana River (1989–93) and Copper River basins (1989–94), Alaska.

Effect	df	Mean square	F	P
River basin	1	4.3	5.8	0.017
Subbasin	4	6.7	9.0	0.0001
Error (A)	222	0.7		
Year	5	1.8	3.3	0.0066
Year × river basin	4	0.9	1.6	0.18
Year × subbasin	18	1.4	2.5	0.0007
Error (B)	490	0.6		

RESULTS

We located 231 different bald eagle nesting territories that were occupied for ≥1 year, 83 in the Gulkana River basin and 148 in the Copper River basin. We observed 274 and 471 nesting attempts in the Gulkana River and Copper River basins. Almost all territories surveyed (97%) were active (i.e., adults laid eggs or were observed in an incubating posture). For both basins and all years combined (n = 745), productivity ($\bar{x}$ ± SE) of bald eagles averaged 0.77 ± 0.03 young fledged per occupied territory and brood size averaged 1.47 ± 0.03 young fledged per successful territory with 52% nest success. Modal brood size of successful nests was the same for both basins (1 young; 54% of nests), but varied by year (Fig. 1). In the Gulkana Basin in 1989 and 1990, 92% of nest failures (n = 25) occurred during incubation whereas only 8% did so after young hatched.

Reproductive Success

Productivity.—Eagle productivity was higher in the Gulkana Basin than the Copper Basin ($\bar{x}$ difference = 0.15 young fledged/occupied territory; Tables 1 and 2). Within river basins productivity varied among subbasins and among years (subbasin × yr interaction $P < 0.001$, Tables 1–3). In the Gulkana Basin, productivity was higher in the Middle Fork subbasin than in either the Main Stem or West Fork subbasins (Table 1). Productivity was similar among years except for 1990 when it was lower than all other years ($P < 0.05$) because of low nesting success (Fig. 2, Table 3). In the Copper Basin, productivity was always lowest in the Middle Copper River subbasin, and most variable across years

Table 1. Number of territories, nesting attempts, productivity and nest success of bald eagles within subbasins of the Gulkana (1989–93) and Copper River basins (1989–94), Alaska.

River basin Subbasin	Nesting territories[a]	Nesting attempts observed	Young fledged/ occupied territory $\bar{x}$	Young fledged/ occupied territory SE	Young fledged/ successful territory $\bar{x}$	Young fledged/ successful territory SE	Nest success (%)
Gulkana							
Main Stem	21	101	0.96 B[b]	0.09	1.53	0.07	62
Middle Fork	7	26	1.27 A	0.15	1.50	0.13	85
West Fork	36	147	0.73 B	0.07	1.44	0.05	52
All subbasins	64	274	0.86	0.05	1.48	0.04	59
Copper							
Upper	15	64	0.91 A	0.11	1.55	0.07	59
Middle	36	168	0.44 B	0.05	1.40	0.06	32
Lower	51	239	0.84 A	0.05	1.49	0.04	57
All subbasins	102	471	0.71	0.04	1.48	0.03	48

[a] Max. no. of uniquely occupied territories observed in any 1 yr.

[b] Within a river basin, means followed by different letters are significantly different ($P < 0.05$, REGWQ Multiple Range Test).

Table 3. Productivity, brood size of successful nests, and nest success of bald eagles in the Gulkana River and Copper River basins, Alaska.

River basin Year	Occupied territories (n)	Young fledged/ occupied territory $\bar{x}$	SE	Young fledged/ successful territory $\bar{x}$	SE	Nest success (%)
Gulkana						
1989	38	1.16 A[a]	0.14	1.65	0.09	68
1990	57	0.53 B	0.09	1.29	0.09	42
1991	58	0.91 A	0.12	1.54	0.10	60
1992	57	0.97 A	0.10	1.40	0.08	69
1993	63	0.86 A	0.11	1.50	0.08	57
Copper						
1989	36	0.81 A	0.14	1.49	0.08	56
1990	70	0.77 A	0.11	1.66	0.08	47
1991	82	0.54 A	0.08	1.34	0.08	40
1992	94	0.76 A	0.09	1.48	0.07	50
1993	94	0.81 A	0.09	1.52	0.07	53
1994	95	0.62 A	0.08	1.36	0.07	45

[a] Within a river basin, means followed by different letters are significantly different ($P < 0.05$, REGWQ Multiple Range Test).

in the Upper subbasin (Table 3). Although productivity of occupied nests varied both spatially and annually, average brood size of successful nests ($n = 454$) was nearly identical in both basins (Table 1) and did not vary appreciably with year or subbasin ($P > 0.19$), except for a slight year × basin effect ($P = 0.093$). This lack of substantial variability in brood size indicates that nest success was the most important determinant of overall productivity.

Nest Success.—Nest success varied by river basin ($\chi^2 = 5.7$, $P = 0.017$) and subbasin ($\chi^2 = 18.8$, $P < 0.001$), but not by year or year × basin interaction ($P > 0.65$) (Tables 1 and 3). Eagles were more likely to nest successfully in the Gulkana (59%, odds ratio = 1.4) than in the Copper Basin (48%, odds ratio = 1.0). In the Gulkana Basin, nests were more likely to be successful ($P = 0.051$) in the Middle Fork subbasin (odds ratio = 5.0) compared to the Main Stem (1.0) or West Fork subbasins (1.5), which paralleled results from productivity analyses. In the Copper Basin, nests were less likely to be successful ($P = 0.008$) in the Middle Copper subbasin (odds ratio = 0.3) compared to the Upper (1.0) or Lower Copper subbasins (0.9).

Territory Occupancy

Territory occupancy rates were identical for eagles in the Gulkana (77%, 292 of 379) and Copper basins (77%, 524 of 685) ($P = 0.82$), and did not vary by year ($P = 0.26$). Within the Gulkana Basin, however, territory occupancy rates varied by subbasin ($P = 0.053$) and were highest ($P = 0.014$) in the Main Stem subbasin (85%, odds ratio = 2.1) compared to both the West Fork (70%, 1.0) and Middle Fork (74%, 1.0) subbasins. In the Copper Basin, territory occupancy rates were similar ($P > 0.27$) among subbasins (range = 74–79%).

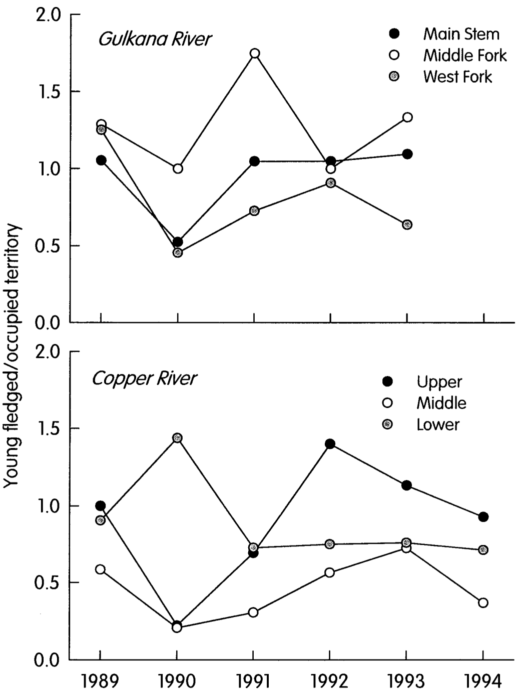

Fig. 2. Annual and spatial (basin and subbasin) variability in productivity of bald eagles from the Gulkana River and Copper River basins.

Intraterritory Variation

Patterns in intraterritory variability were similar for eagles along both rivers, so we combined data for analyses. Whether or not a pair was successful in a given year was associated strongly with nest success, territory occupancy, and choice of nest location the previous year (assuming pairs were site faithful; Gerrard et al. 1992, Jenkins 1992). Pairs that were successful one year were more likely to be successful the following year (62%, $n = 292$) compared to those that had been unsuccessful (48%, $n = 191$; $\chi^2 = 9.2$, $P = 0.002$). Pairs that were successful one year had higher productivity the following year (0.89 ± 0.05, $n = 292$) compared to those that had been unsuccessful (0.72 ± 0.06, $n = 191$; $t = 2.3$, $P = 0.025$). Pairs that were successful one year were more likely to reoccupy their territory the following year (60%, $n = 605$) compared to those that had been unsuccessful (40%; $\chi^2 = 14.2$, $P < 0.001$). Further, pairs that were successful one year were more likely to reuse the same nest tree the following year (68%, $n = 484$) compared to those that had been unsuccessful (32%; $\chi^2 = 34.8$, $P < 0.001$). Within territories, there was no correlation between brood size in successive years for pairs successful in both years ($r = 0.02$, $P = 0.8$, $n = 180$).

Spring Weather and Salmon Abundance

If reproductive success was related to severity of spring weather (92% of nesting failure in the Gulkana Basin occurred in spring), we would expect productivity or nest success to be correlated positively with temperature or correlated negatively with amount of precipitation. On a subbasin-level, however, neither productivity nor nest success was correlated with amount of precipitation in May ($r = <0.02$, $P > 0.9$, $n = 33$). Productivity ($r = -0.30$, $P = 0.09$) and nest success ($r = -0.30$, $P = 0.02$) were correlated negatively with average ambient temperature in May (opposite of what we predicted), suggesting that these elements of spring weather did not influence eagle reproductive success predictably during our study. There was a correlation between eagle productivity and escapement of sockeye salmon in the Gulkana Basin ($r = 0.90$, $P = 0.10$) but not in the Copper Basin ($r = -0.08$, $P = 0.88$). However, there were no correlations between escapement of sockeye and nest success or escapement of chinook salmon with productivity or nest success for either basin ($P > 0.23$; power = 0.39 to detect $r = 0.6$ with $\alpha = 0.10$).

Comparing Reproductive Success among Populations

Productivity, brood size of successful nests, and nest success are important parameters often used to describe the reproductive dynamics of bald eagle and other raptor populations. Sprunt et al. (1973) suggested that eagle populations meeting or exceeding some value for both productivity (1.0) and nest success (50%) can be considered "stable." However, if population stability can be gauged by the reproductive output of a population (total no. young produced)—which is implicit in Sprunt et al.'s (1973) definition—then any product of nest success and productivity that equals 50 will yield the identical level of reproductive output (e.g., 1.0 × 50% = 50; 0.9 × 55%; 1.1 × 45%). Population stability therefore can be achieved in combinations other than the one suggested by Sprunt et al. (1973) because productivity and nest success are highly correlated ($r_s = 0.80$, $P < 0.0001$, $n = 18$; Table 4) and consequently provide much of the same information. The lack of a perfect correlation between these 2 parameters results solely from differences in brood size, which is not correlated with nest success ($r_s = 0.10$, $P = 0.69$). Because productivity represents the product of brood size and nest success, we suggest that productivity be used when a simplistic measure is needed to compare reproductive output among populations. Hence, when considered as a group, bald eagles nesting in the Gulkana Basin ($\bar{x}$ productivity = 0.86) were reproducing at levels comparable to other populations ($\bar{x} = 0.94$), whereas those nesting in the Copper Basin ($\bar{x} = 0.71$) were reproducing at levels lower than all other eagle populations examined (Table 4).

DISCUSSION

Reproductive success of these northern bald eagle populations varied at several scales, from within individual nesting territories, where previous reproductive success influenced current reproductive success, to larger spatial (basin and subbasin) and temporal (annual) scales, both within and between populations. Within a territory, pairs that were successful one year had higher nest success, higher productivity, higher territory reoccupancy rates, and were more likely to reuse the same nest the following year. These within-territory effects suggest that either the resident pair or features of the territory (or both) influence reproductive success of these eagle populations. Within both of the populations we studied, there was considerable annual and spatial variation in reproduction (Tables 1–3), a result that parallels other studies from throughout the bald eagles' range (Grubb et al. 1983, Isaacs et al. 1983, McAllister et al. 1986, Swenson et al. 1986; Table 4). Most of the variability we observed in reproductive success resulted from differences in the proportion of nesting attempts that were successful rather than differences in brood sizes of successful pairs.

Geographical differences in reproductive success of bald eagles (Sprunt et al. 1973, Grubb et al. 1983, this study) are likely a result of dif-

Table 4. Reproductive parameters of bald eagle populations. We excluded data from populations where authors indicated environmental contaminants were a potentially significant problem.

Geographic region	Occupied territories (n)	Young fledged/ occupied territory	Young fledged/ successful territory[a]	Nest success (%)	Study period	Source
Inland Wis.	1,469	1.30	1.69	77	1983–88	Kozie and Anderson (1991)
Colorado and Wyoming	85	1.21	1.92	63	1981–89	Kralovec et al. (1992)
Saskatchewan, Can.	264[b]	1.17	1.60	73	1973–81	Gerrard et al. (1983)
Saskatchewan, Can.	48	1.06	1.82	58	1984–87	Dzus and Gerrard (1993)
Yukon Territory, Can.	39	1.05	1.46	72	1980–82	Blood and Anweiler (1990)
Kodiak Island, Alas.	312	1.00	1.59	63	1963–70	Sprunt et al. (1973)
Wisconsin	492	1.00	1.52	66	1962–70	Sprunt et al. (1973)
Yellowstone Ecosystem	232	0.98	1.63	60	1976–82	Swenson et al. (1986)
Oregon	606	0.92	1.37	67	1978–82	Isaacs et al. (1983)
Washington	866	0.87	1.32	66	1981–85	McAllister et al. (1986)
Gulkana River, Alas.	274	0.86	1.48	59	1989–93	This study
Amchitka, Alas.	68	0.86	1.43	60	1969–84	Sherrod et al. (1976)
San Juan Islands, Wash.	275	0.84	1.35	62	1975–80	Grubb et al. (1983)
California	140	0.81	1.45	56	1970–91	Jenkins (1992)
Arizona	45	0.80	1.63	49	1975–80	Grubb et al. (1983)
New Brunswick, Can.	55	0.73	1.33	55	1974–80	Stocek and Pearce (1981)
Coastal Florida	592	0.73	1.46	50	1961–70	Sprunt et al. (1973)
Copper River, Alas.	471	0.71	1.48	48	1989–94	This study

[a] Young fledged/successful territory calculated as young fledged/occupied territory ÷ nest success.

[b] Using midpoint of estimates.

ferences in habitat quality, including factors such as weather, breeding-season length, nesting density, human disturbance, environmental contaminants, and prey abundance. One obvious difference in habitat between the Gulkana River and Copper River basins is in the character of the rivers themselves. Waters of the Gulkana River are clear, whereas those in most of the Copper River are glacial and carry high silt-loads resulting in extreme turbidity. This contrast may partially explain differences in reproductive success through differential availability of fish, which constitutes the major portion of eagle diets during the breeding season in the Gulkana Basin (R. J. Steidl and R. G. Anthony, unpubl. data).

Differences in levels of human disturbance, weather, and some indicator of prey abundance have explained variability in reproductive success and nesting activity of bald eagle populations previously (McEwan and Hirth 1979, Swenson et al. 1986, Hansen 1987). The effects of human activity on bald eagle reproduction have been ambiguous, largely because the intensity, types, and timing of disturbances often differ among studies (Steidl 1995). Within the Gulkana Basin, there was a negative correlation between the level of human activity and eagle reproduction in each subbasin ($r = -0.90$, $P = 0.037$; Steidl 1995); however, this analysis included nesting failures that occurred during incubation, and levels of human activity did not become appreciable until several weeks after hatching. Elsewhere, individual years of low productivity have been associated with inclement spring conditions (Swenson et al. 1986, Gerrard et al. 1992). We found no relation between reproductive success and spring weather conditions in our study areas, suggesting that differences in spring weather were not associated strongly with the variability we observed in reproductive success during our study.

One possibility that we could not address adequately is that reproductive success might be regulated by annual and spatial differences in levels of prey abundance at different periods in the breeding cycle. Although the correlation between salmon escapement and reproductive success was inconsistent, salmon do not enter rivers to spawn until several weeks after nestlings hatch. Because most nesting failure occurred during incubation, this finding is not unexpected. However, other evidence suggests that prey levels can control bald eagle reproductive rates, especially in northern populations. Nesting activity, nestling survival, and therefore productivity, increased when prey was placed within nesting territories of bald eagles in southeastern Alaska (Hansen 1987). A difference in densities of bald eagles breeding along

2 northern lakes also was associated with a difference in prey characteristics (Dzus and Gerrard 1993). Lastly, variability in breeding rates of eagles in southeastern Alaska (14–84% breed/yr) was attributed to variability in prey abundance (Hansen and Hodges 1985). Therefore, variability in nesting success observed in interior Alaska and elsewhere may have been related to prey availability. Further, because most nesting failure occurred before hatching in our study and in others (Fraser 1981), the level of prey availability before and during incubation seems most critical. This period of the breeding season corresponds roughly to when lakes and rivers become free of ice in our study areas. Severe spring temperatures might affect availability of fish if break-up of winter ice is delayed; alternatively, the abundance of ungulate carcasses might be higher in years with heavy snowfalls and provide food for eagles when they arrive in nesting areas. Availability of seasonally abundant prey during eagle migration and early in incubation, such as eulachon (*Thaleichthys pacificus*), snowshoe hare (*Lepus americanus*), or migratory birds, may also affect breeding condition and reproductive success.

Our speculation that reproductive success might be influenced by prey availability early in the breeding season is supported further by the lack of any correlation between reproductive success and salmon abundance during brood rearing, and because brood sizes of successful nests showed little annual variability (Table 3) despite biologically important differences in reproductive success between basins. If annual and spatial differences in prey levels during the nestling period were important, brood size also would vary annually and spatially because brood reduction occurs in populations of eagles (Bortolotti 1986) and other raptors (Steidl and Griffin 1991) where prey is somehow limited. Thus, we hypothesize that prey availability before and during incubation, perhaps regulated by spring severity or other factors, might be responsible for the observed variation in reproductive success of these northern bald eagle populations.

MANAGEMENT IMPLICATIONS

Most bald eagles in Alaska inhabit nearly pristine habitats. Their reproductive performance is therefore representative of northern regions that have not been altered significantly by humans. The substantial variability in reproductive success we observed in these populations may result because eagles are nesting near the limits of their geographical range and therefore are susceptible to the considerable fluctuations in prey and weather. To better understand how prey abundance influences bald eagle reproduction, we recommend that prey consumed during preincubation and incubation periods be identified and prey populations levels be monitored annually, or a supplemental-prey experiment be conducted.

Researchers and managers who choose to monitor bald eagle populations and productivity must recognize that efforts to detect trends in these parameters require relatively long time commitments that are necessary to reduce potential biases caused by the high variability in reproductive success of these long-lived birds. Statistical power to detect trends in eagle population parameters is likely to be low with even 10 years of data (Hatfield et al. 1996). However, aerial productivity surveys are simple, efficient, and relatively inexpensive to perform. In addition to providing data on reproductive success, these surveys also yield information on population size, density, distribution, territory occupancy rates, and within-territory rates of nest changing, all of which provide insights on population processes.

LITERATURE CITED

BENT, A. C. 1937. Life histories of North American birds of prey. I. Dover Publ., New York, N.Y. 409pp.

BLOOD, D. A., AND G. C. ANWEILER. 1990. Nesting chronology and success of bald eagles in southwest Yukon. Northwest. Nat. 71:9–11.

BORTOLOTTI, G. R. 1986. Evolution of growth rates in eagles: sibling competition vs. energy considerations. Ecology 67:182–194.

COLLETT, D. 1991. Modelling binary data. Chapman and Hall, New York, N.Y. 369pp.

DZUS, E. H., AND J. M. GERRARD. 1993. Factors influencing bald eagle densities in northcentral Saskatchewan. J. Wildl. Manage. 57:771–778.

FRASER, J. D. 1981. The breeding biology and status of the bald eagle on the Chippewa National Forest. Ph.D. Thesis, Univ. Minnesota, St. Paul. 235pp.

GERRARD, J. M., AND G. R. BORTOLOTTI. 1988. The bald eagle: haunts and habits of a wilderness monarch. Smithsonian Inst. Press, Washington, D.C. 177pp.

———, P. N. GERRARD, G. R. BORTOLOTTI, AND D. W. A. WHITFIELD. 1983. A 14-year study of bald eagle reproduction on Besnard Lake, Saskatchewan. Pages 47–57 *in* D. M. Bird, ed. Biology and management of bald eagles and ospreys. Harpell Press, Ste. Anne de Bellevue, Que. 325pp.

———, ———, ———, AND E. H. DZUS. 1992. A

24-year study of bald eagles on Besnard Lake, Saskatchewan. J. Raptor Res. 26:159–166.

GRUBB, T. G., R. L. KNIGHT, D. M. RUBINK, AND C. H. NASH. 1983. A five-year comparison of bald eagle productivity in Washington and Arizona. Pages 35–45 *in* D. M. Bird, ed. Biology and management of bald eagles and ospreys. Harpell Press, Ste. Anne de Bellevue, Que. 325pp.

HANSEN, A. J. 1987. Regulation of bald eagle reproductive rates in southeast Alaska. Ecology 68: 1387–1392.

———, AND J. I. HODGES. 1985. High rates of nonbreeding adult bald eagles in southeastern Alaska. J. Wildl. Manage. 49:454–458.

HATFIELD, J. S., W. R. GOULD IV, B. A. HOOVER, M. R. FULLER, AND E. L. LINDQUIST. 1996. Detecting trends in raptor counts: power and Type I error rates of various statistical tests. Wildl. Soc. Bull. 24:505–515.

ISAACS, F. B., R. G. ANTHONY, AND R. J. ANDERSON. 1983. Distribution and productivity of nesting bald eagles in Oregon, 1978–1982. Murrelet 64: 33–38.

JENKINS, J. M. 1992. Ecology and behavior of a resident population of bald eagles. Ph.D. Thesis, Univ. California, Davis. 183pp.

KOZIE, K. D., AND R. K. ANDERSON. 1991. Productivity, diet, and environmental contaminants in bald eagles nesting near the Wisconsin shoreline of Lake Superior. Arch. Environ. Contam. Toxicol. 20:41–48.

KRALOVEC, M. L., R. L. KNIGHT, G. R. CRAIG, AND R. G. MCLEAN. 1992. Nesting productivity, food habits, and nest sites of bald eagles in Colorado and southeastern Wyoming. Southwest. Nat. 37: 356–361.

MCALLISTER, K. R., T. E. OWENS, L. LESCHNER, AND E. CUMMINS. 1986. Distribution and productivity of nesting bald eagles in Washington, 1981–1985. Murrelet 67:45–50.

MCEWAN, L. C., AND D. H. HIRTH. 1979. Southern bald eagle productivity and nest site selection. J. Wildl. Manage. 43:585–594.

POSTUPALSKY, S. 1974. Raptor reproductive success: some problems with methods, criteria, and terminology. Pages 21–31 *in* F. N. Hamerstrom, Jr., B. E. Harrell, and R. R. Olendorff, eds. Management of raptors. Proc. Conf. Raptor Conserv. Tech. Raptor Res. Rep. 2.

RITCHIE, R. J., AND S. AMBROSE. 1996. Distribution and population status of bald eagles (*Haliaeetus leucocephalus*) in interior Alaska. Arctic 49:120–128.

SCHEMPF, P. 1989. Raptors in Alaska. Pages 144–154 *in* B. G Pendleton, ed. Proc. Western raptor management symposium and workshop. Nat. Wildl. Fed. Sci. Tech. Ser. 12.

SHERROD, S. K., C. M. WHITE, AND F. S. L. WILLIAMSON. 1976. Biology of the bald eagle on Amchitka Island, Alaska. Living Bird 15:143–182.

SPRUNT, A. IV, W. B. ROBERTSON, JR., S. POSTUPALSKY, R. J. HENSEL, C. E. KNODER, AND F. J. LIGAS. 1973. Comparative productivity of six bald eagle populations. Trans. North Am. Wildl. Nat. Resour. Conf. 38:96–106.

STALMASTER, M. V. 1987. The bald eagle. Universe Books, New York, N.Y. 227pp.

STEIDL, R. J. 1995. Human impacts on the ecology of bald eagles in interior Alaska. Ph.D. Thesis, Oregon State Univ., Corvallis. 155pp.

———, AND C. R. GRIFFIN. 1991. Growth and brood reduction of mid-Atlantic coast ospreys. Auk 108:363–370.

STOCEK, R. F., AND P. A. PEARCE. 1981. Status and breeding success of New Brunswick bald eagles. Can. Field-Nat. 95:428–433.

SWENSON, J. E., K. L. ALT, AND R. L. ENG. 1986. Ecology of bald eagles in the Greater Yellowstone ecosystem. Wildl. Monogr. 95. 46pp.

Received 11 September 1995.
Accepted 22 May 1997.
Associate Editor: Noon.